

Decomposition of *Metrosideros polymorpha* leaf litter along elevational gradients in Hawaii

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Abstract

We examined interactions between temperature, soil development, and decomposition on three elevational gradients, the upper and lower ends of each being situated on a common lava flow or ash deposit. We used the reciprocal transplant technique to estimate decomposition rates of *Metrosideros polymorpha* leaf litter during a three-year period at warm and cool ends of each gradient. Litter quality was poorest early in soil development or where soils were most intensely leached and waterlogged. *In situ* litter decomposition was slowest on the young 1855 flow ($k=0.26$ and 0.14 at low and high elevation, respectively). The more fertile Laupahoehoe gradient also supported more rapid *in situ* decay at the warmer low elevation site ($k=0.90$) than at high elevation ($k=0.51$). The gradient with the most advanced soil development showed no difference for *in situ* decay at low and high elevations ($k=0.88$ and 0.99 , respectively) probably due to low soil nutrient availability at low elevation, which counteracted the effect of warmer temperature. Comparisons of *in situ*, common litter, and common site experiments indicated that site factors influenced decomposition more than litter quality did. The effect of temperature, however, could be over-ridden by soil fertility or other site factors. Field gradient studies of this sort yield variable estimates of apparent Q_{10} , even under the best conditions, due to interactions among temperature, moisture, nutrient availability, decomposer communities and litter quality. Such interactions may be as likely to occur with changing climate as they are along elevational gradients.

Keywords: Hawaii, litter quality, *Metrosideros polymorpha*, tropical montane rain forest, site fertility, ecosystem development

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Introduction

Decomposition is controlled by temperature, moisture, the chemistry of the organic material, and the composition and dynamics of the decomposer community (Swift *et al.* 1979). The effects of temperature are particularly interesting, because anthropogenic climate change, caused primarily by increased atmospheric CO₂ concentrations, has the potential to accelerate rates of decomposition, thereby providing a positive feedback to increased CO₂ (Schimel *et al.* 1990; Townsend *et al.* 1992). Decomposition also drives the release of organically bound nutrients into biologically available forms: thus enhanced rates of decomposition also could allow

offsetting storage of C due to increased growth of nutrient-limited vegetation (Schimel *et al.* 1990; Melillo *et al.* 1993).

A recent field study of litter decomposition in the Hawaiian Islands indicated that rate of decomposition increased four to eleven-fold for a 10 °C increase in temperature, depending on the sites and substrates (Vitousek *et al.* 1994). That study was carried out on two individual lava flows that reached from above tree line to near the sea. The flows represented unusually clean single-age, single-substrate transects across a well-defined range in temperature. Moreover, that study made use of a single widely distributed tree species, *Metrosideros polymorpha* that dominated all of the sites. Consequently, it would seem to represent a better-

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constrained field study than could be carried out in most environments. What caused the large apparent sensitivity of decomposition to temperature?

Vitousek *et al.* (1994) suggested that one possible reason for the rapid increase in decomposition with increasing temperature was systematic variation in nutrient availability with elevation and temperature. The lava flows they studied were relatively young (135 and ~3400 y old). The rate of ecosystem development on these flows varied as a function of climate, with much more rapid accumulation of plant biomass and soil organic matter at low elevation/high temperature (Aplet & Vitousek 1994; Raich *et al.* 1997). Moreover, nutrient availability and leaf litter chemistry varied as a function of ecosystem development, with relatively low nutrient availability and strong nutrient limitation to plant growth in young sites (Crews *et al.* 1995; Raich *et al.* 1996; Vitousek & Farrington 1997). Accordingly, the higher-elevation sites on a given flow were at an earlier developmental stage than lower-elevation sites on the same flow, and an interaction between low temperature, low nutrient availability, litter chemistry, and possibly the decomposer community could have steepened the apparent response of decomposition to temperature in these sites. This interaction would not be unique to Hawaiian ecosystems; Tanner *et al.* (1998) suggested that nutrient availability could be reduced systematically in montane as opposed to lowland tropical forests, and nitrogen limitation, in particular, could be more widespread in cool montane sites.

We examined possible interactions between temperature, ecosystem development, and decomposition by focusing on two elevational gradients on substrates older than those evaluated by Vitousek *et al.* (1994). We expected more advanced soil development at these sites than on the younger lava flows they studied, and so less contrast in developmental stage between high and low

elevations within a gradient. This study was designed as a follow-up to Vitousek *et al.* (1994); therefore, we used the same dominant species, and we repeated their measurements at two elevations on their younger flow. Our measurements also were conducted in parallel with a study of decomposition on a very long gradient of soil and ecosystem development (Crews *et al.* 1995), so our discussion can draw upon a broader range of sites and litter types than just the three elevational gradients.

Methods

Study sites

This research was carried out on the windward sides of the islands of Maui and Hawaii, in *Metrosideros*-dominated rainforest. The climate of these slopes is moist to wet subtropical. The study areas are exposed to the prevailing north-east trade winds; rainfall reaches a maximum between 700 and 1000 m elevation, and exceeds 2000 mm y⁻¹ from sea level to the trade-wind inversion, which oscillates between c. 1900 and 2400 m elevation (Giambelluca & Nullet 1991). Above the inversion, precipitation decreases rapidly, and evaporative demand increases substantially. The mean annual temperature at sea level is ~24 °C, and temperature decreases with increasing elevation up to the trade-wind inversion at a mean annual lapse rate of ~6.4 °C per 1000 m (Juvik & Nullet 1994; Department of Geography, University of Hawaii at Hilo 1998).

We measured decomposition in high (1550–1780 m) and low (410–915 m) elevation sites (Table 1) on the windward north and east flanks of the large volcanoes Mauna Loa and Mauna Kea (island of Hawaii) and Haleakala (island of Maui). All three mountains reached well above tree line. The resultant climate–age matrix has been well characterized geologically and climatologically

Table 1 Location and climatic and edaphic characteristics of study sites

Site	Island	Elevation (m)	Mean annual temp. ¹ (°C)	Mean annual precip. ² (mm)	Soil taxonomic group	Relative soil N and P availability ³
1855 flow	Hawaii	700	20.0	6000	Lithic Tropofolist	Low
1855 flow	Hawaii	1660	14.5	2600	Lithic Tropofolists	Very low
Laupahoehoe flow	Hawaii	915	18.8	3500	Typic Hydrandepts	High
Laupahoehoe flow	Hawaii	1555	15.1	2200	Hydric Dystrandepts	High
Waikamoi	Maui	410	21.7	4500	Histic Plaquepts	Low
Waikamoi	Maui	1780	13.9	2200	Typic Hydrandepts	High
Kilauea	Hawaii	1190	17.2	2500	Hydric Dystrandepts	Low

¹Department of Geography, University of Hawaii at Hilo 1998; ²Giambelluca *et al.* 1986; ³Based on foliar nutrients, and soil nutrient availability measurements in Crews *et al.* 1995, Kitayama & Mueller-Dombois 1994a, Kitayama *et al.* 1998, Raich *et al.* 1997, and Townsend *et al.* 1995.

(Lockwood *et al.* 1988; Nullet *et al.* 1995), and numerous ecological studies have made use of these systems (e.g. Vitousek *et al.* 1992, 1994; Drake & Mueller-Dombois 1993; Raich *et al.* 1997; Aplet *et al.* 1998).

On Mauna Loa, an active shield volcano with frequent lava flows that cover a broad range of elevations and aspects, we selected sites on an 1855 flow at 700-m and 1660-m elevation; the sites were near those used by Vitousek *et al.* (1994). The sites on Mauna Kea were on the c. 5000-y-old Kanakaleonui lava flow that reaches from above tree line to the sea in the Laupahoehoe Forest Reserve (Wolfe & Morris 1996). On this flow, the forest has been converted to pasture below 700-m and above 1650-m elevation. We used sites in *Metrosideros*-dominated native forest at 915 m and 1555 m. Soil fertility and plant nutrient concentrations are substantially higher on this flow than on the younger flows on Mauna Loa (Crews *et al.* 1995; Townsend *et al.* 1995; Vitousek *et al.* 1995). Mean annual rainfall ranges from c. 2000 mm to 3500 mm within the forested area of Laupahoehoe (Giambelluca *et al.* 1986).

High- and low-elevation sites also were selected in the Waikamoi area on the north slope of Haleakala Volcano, island of Maui. Kitayama & Mueller-Dombois (1994a,b) evaluated the vegetation and soils of the area; we used their 410-m and 1780-m sites in this study. Annual rainfall is near 4500 mm at the low site and over 2000 mm at the high site. Soils on Haleakala are older and much more highly developed than those on Mauna Loa or Mauna Kea. Soil fertility and plant nutrient contents are greater at the high- than the low-elevation Waikamoi site (Kitayama & Mueller-Dombois 1994a), the reverse of the pattern on young Mauna Loa lava flows. This inversion may reflect the fact that soil development in the low wet site has proceeded past the point of maximum soil fertility and into a declining phase characterized by a substantial depletion of nutrients (Walker & Syers 1976; Vitousek *et al.* 1997). It may also reflect waterlogged conditions at low elevation where drainage is poor due to gently sloping topography and presence of an iron hardpan (Kitayama & Mueller-Dombois 1994a; Kitayama *et al.* 1998).

Finally, we used the Kilauea rainforest site, adjacent to Hawaii Volcanoes National Park, as a well-protected common site in which litter from all the sites could be decomposed under constant conditions. The Kilauea site is the youngest on the soil developmental sequence described by Crews *et al.* (1995); it is at 1200-m elevation and annually averages 2500 mm of precipitation.

Despite the wide range of temperatures and soil developmental states considered here, all of the sites had several characteristics in common: the native tree, *Metrosideros polymorpha*, dominated each; their soils were developed in basaltic parent material from the Hawaiian volcanic hot spot; they were on the constructional surface

of shield volcanoes; they had not been cleared or subjected to other systematic human disturbance. Accordingly, research on these sites can keep many potentially significant factors nearly constant, while substantially varying temperature and soil developmental status.

Field and laboratory techniques

The reciprocal transplant technique (Hirschfeld *et al.* 1984; Vitousek *et al.* 1994) was used to examine the separate and combined effects of site and substrate quality on weight loss and nutrient dynamics of decaying *Metrosideros* leaves. The combined effect of these factors was examined by following the decay of senescent leaves at their site of origin, hereafter termed *in situ* leaves. The effect of site environment was evaluated by following decay of senescent leaves collected from one site (1855 low-elevation site) and set out at each of the other sites, hereafter termed common leaves. The common leaves controlled for variation in litter quality (the inherent decomposability of litter), thus providing a cleaner test of the effects of site differences (including temperature) on decomposition. However, the *in situ* litter provided a more direct integrated measure of the long-term effects of differing temperatures, in that climatic change ultimately could affect litter quality and nutrient availability as well as decomposition itself. The effect of substrate quality was examined by following decay of leaf litter from all sites set out at a single site (Kilauea rain forest site), hereafter termed common site.

We used litter bags to determine rates of leaf decomposition. Bags were 18 cm × 20 cm and constructed of fibreglass screen with a mesh size of 1.5 mm. Although mesh bags alter litter moisture regimes, we chose the method over the tethered-leaf technique used by Vitousek *et al.* (1994) because (i) it minimized the problem of distinguishing between decomposition and comminution, a problem that worsens as decay progresses, and (ii) previous study (Scowcroft 1997) showed that earthworms, millipedes, and other small litter-feeding invertebrates had ready access to bag contents.

Leaf litter from each site was collected in litter traps that were emptied weekly during the period November–December 1991. Collections were air-dried in the laboratory for at least two weeks to bring them to relatively uniform moisture content. Mesh bags were filled with about 1 g air-dried litter. In January 1992, these bags were distributed among the sites as follows: 30 bags were placed in the site where they were collected (*in situ* leaves); 20 bags from each site were placed in the Kilauea site (common site); and 30 bags of litter from the 1855 low elevation flow were placed in each of the other sites (common leaves). Sub-samples of initial collections

were oven-dried at 70°C to a constant weight to determine air-dry:oven-dry ratios and initial chemical compositions (N, P, K, Ca, Mg, and lignin).

We retrieved three to five litter bags of each type at about 1, 3, 6, 12, 18, 24, 30, and 36 months after emplacement. Bag contents were oven-dried (70°C), weighed, and ground for chemical analysis. Total nitrogen and phosphorus in undecomposed and partially decomposed litter were determined colourimetrically after persulphate (Kjeldahl) digestion in a block digester. Potassium, calcium, and magnesium levels were determined at 12 and 18 months only by atomic absorption spectrophotometer after dry ashing in a muffle furnace at 550°C. Initial concentrations of lignin were determined using the procedure of Van Soest & Wine (1968).

The first-order exponential decay model (Wieder & Lang 1982) was fitted to the decomposition data for each litter type using the SAS procedure NLIN (SAS Institute 1985). The model was $W/W_0 = e^{-kt}$, where W is the dry weight remaining at time t , W_0 is the initial dry weight, and k is the decay constant.

For each experiment, significant differences among decay constants were determined using the Games & Howell (1976) procedure for multiple pairwise comparisons ($\alpha = 0.05$). Analyses of variance were used to examine differences in nutrient dynamics among sites or among sources of litter. The Bonferroni method for pairwise comparisons was used to evaluate differences among means ($\alpha = 0.05$). Our sample sizes were small, and this made it difficult to differentiate among treatment means. This difficulty became greater as the study progressed because too little of some samples remained for chemical analyses, even though dry weight could be determined.

Results

Weather variables

Temperatures at our study sites were assumed to be close to those recorded at representative standard meteorological stations located below the inversion layer and on windward slopes (Fig. 1a). The annual lapse rate using these data was $\approx 6.2^\circ\text{C}$ per 1000 m. Temperature data collected by Juvik & Nullet (1994) during the first year and a half of our study along the 1855 flow showed strong agreement (6.4°C per 1000 m) with the data in Fig. 1(a), and validated our assumption.

El Niño events in 1992 and 1993 resulted in below normal rainfall during January–May throughout Hawaii. On windward sides of Hawaii and Maui rainfall was 10% to 50% of normal. Juvik & Nullet (1994) reported 0.5% normal rainfall at 1640-m elevation on the 1855 flow during January–February 1992 (Fig. 1b). As El Niño

weakened, rainfall intensified and exceeded 600 mm several months at low elevation on the 1855 flow (Fig. 1c).

Litter chemistry

Nitrogen and phosphorus concentrations in *Metrosideros* leaf litter were strongly correlated (Fig. 2a) and varied from 0.27 to 1.02% and 0.022–0.067% (for N and P, respectively) across the six sites included in this study (Table 2). N and P were low at both elevations on the 1855 flow, and reached a minimum at the high-elevation site. In contrast, both sites on the Laupahoehoe gradient had much higher N and P concentrations with the high-elevation site producing litter that was significantly richer in these nutrients. At Waikamoi, N and P concentrations were low at low elevation (and not significantly different from those for the 1855 flow), and about two-fold greater at high elevation (and not significantly different from the low-elevation Laupahoehoe site).

Although elevational differences in N and P concentrations on the 1855 flow were not statistically significant, real differences of such a size would be considered important. Based on observations by others we suspect that there are elevational differences but our sample sizes were probably too small to detect them. One would predict more rapid weathering and greater atmospheric deposition at low elevation sites during primary succession (Vitousek *et al.* 1992; Raich *et al.* 1997). Indeed, Vitousek *et al.* (1994) reported a similar pattern on the 3400-y-old Punahoa flow as well as the 1855 flow.

Concentrations of Ca, Mg, and K varied more than two-fold among the sites, generally in an intercorrelated way. Lignin concentrations were near 20% in all of the sites, except that litter in the low-elevation Laupahoehoe site had 26% lignin (Table 2).

Decomposition vs. elevation

On the young 1855 flow, *in situ* litter decayed significantly faster at the low-elevation site (Table 3). The same was true for the Laupahoehoe gradient, but there decomposition was significantly faster at both high and low elevations than along the 1855 flow. In contrast, this elevational effect was not observed on the Waikamoi gradient; in fact *in situ* decomposition at the lower elevation site was slower than at the high-elevation site, although not significantly so.

The common litter provided an identical substrate for decomposition in all of the sites, and thus provided an integrated measure of the effects of site factors on decomposition, including the effects of temperature. On the 1855 flow, the low-elevation (warmer) site supported a faster rate of decomposition of common litter than the high-elevation (cooler) site (Table 3), and the difference

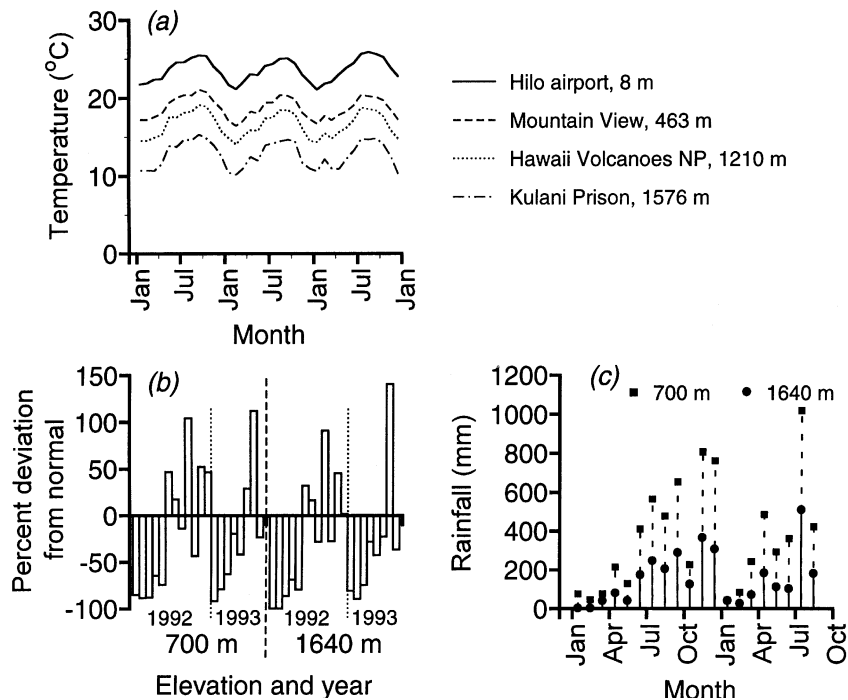


Fig. 1 Mean monthly air temperature (a) from January 1992 to December 1994 for four meteorological stations located below the trade-wind inversion on windward Mauna Loa, island of Hawaii. Percent deviation from normal rainfall (b) and actual/estimated rainfall (c) between January 1992 and August 1993 at 700 m and 1640 m elevations along the 1855 gradient (from Juvik & Nullet 1994).

was only slightly smaller than for *in situ* litter. The same elevational (temperature) pattern was found on the Laupahoehoe gradient, but the difference between high- and low-elevation decay rates was not significant. Like the results for *in situ* litter, decomposition was significantly faster on the Laupahoehoe gradient than on the 1855 gradient, despite their similar temperature regimes. Common litter at the Waikamoi sites also decomposed faster than at the 1855 sites, and rates at Waikamoi were not statistically different.

Litter and site quality

Decomposition of litter collected at each of the sites and set out at the common site provided a direct measure of litter quality, the relative decomposability of litter. We found that litter from the low elevation site on the 1855 flow was recalcitrant ($k=0.35$), and it decayed significantly slower than litter from every other site except low elevation Waikamoi (Table 3). Quality of litter from the more fertile Laupahoehoe flow was significantly better ($k=0.46$ and 0.47) than that from low elevation on the 1855 flow, but not significantly better than that from high elevation on the 1855 flow; and it did not vary with elevation. The high elevation Waikamoi site produced the most readily decomposable litter ($k=0.64$) of any site, while the low Waikamoi site produced low quality litter ($k=0.38$), which was not significantly different from that produced at the low elevation site on the 1855 flow.

Decomposition of litter at the common site was correlated with initial N (Fig. 2b) and P concentrations (not shown). The N and P concentrations of litter were clear indicators of high- and low-quality litter; when N in litter was >0.8 and P was >0.04 , the decomposition constant (k) was >0.45 . Litter from Crews *et al.* (1995) sites followed the same pattern. Lignin concentrations varied little among the sites; even when it was high, 26% at the low-elevation Laupahoehoe site (Table 2), the rate of decomposition was not notably slowed. Decomposition of litter *in situ* was not well correlated with initial N (Fig. 2c) and P concentrations (not shown), indicating that factors other than litter quality were affecting *in situ* decomposition.

We used results of the common site and common leaves experiments to estimate the relative contributions that litter quality and site characteristics (temperature, soil fertility, etc.) made to observed rates of *in situ* decomposition. With the exception of the high-elevation Waikamoi site, decay curves for the common-site experiment (Fig. 3a) were clustered closely about each other, suggesting that litter quality was not exerting great control on decomposition. On the other hand, comparison of the decay curves for the common-leaves experiment (Fig. 3b) with those for the *in situ* experiment (Fig. 3c) shows substantial similarity.

We evaluated the relative importance of site (including nutrient status, temperature, and other factors) on the one hand with litter quality on the other by examining correlations between k values for the *in situ* experiment

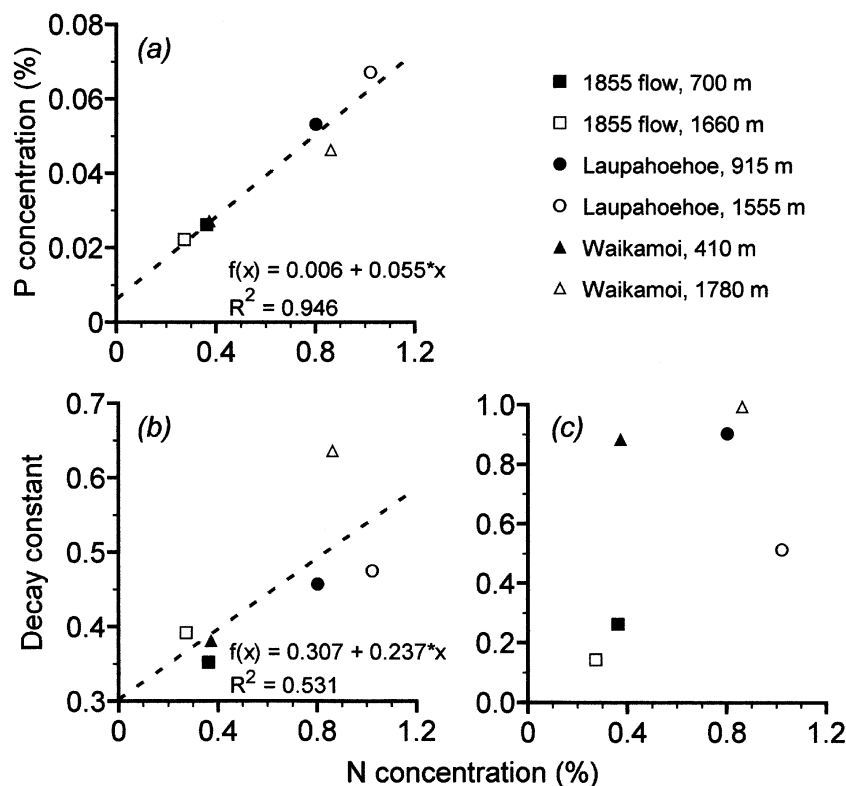


Fig. 2 Relationship between initial nitrogen concentration of *Metrosideros* leaf litter and (a) initial phosphorus concentration of litter (b) decay constants for the common site experiment, and (c) decay constants for the *in situ* litter experiment. Dashed lines represent least squares linear regression fit.

and for the common leaf and the common site experiments. Litter decomposition *in situ* was strongly and positively correlated with site characteristics (Fig. 4a). Decomposition at the sites described by Crews *et al.* (1995) was measured in parallel with the six sites emphasized here, and their findings fit the same pattern we observed. *In situ* decomposition also correlated with relative litter quality (Fig. 4b), but the fit was poorer.

How much of this site effect can be ascribed to temperature? The most direct test of the importance of temperature is the relationship between site temperature and decomposition of the common leaves; this substrate removes any influence of litter quality on the rate of decomposition. We found no correlation between mean annual temperature and decomposition of this litter across the range of sites examined, although within a gradient, the tendency was for more rapid decay at the warmer site (Fig. 5). Instead, low-nutrient sites generally supported lower rates of decomposition than high-nutrient sites. Nutrient status has been assessed with measurements of N and P mineralization in the 1855 sites and near the Laupahoehoe sites (Crews *et al.* 1995; Raich *et al.* 1997), and by nutrient pool measurements in the Waikamoi sites (Kitayama & Mueller-Dombois 1994a). Additionally, foliar and litter N and P concentrations, which were measured at all sites in this study, provide a well-validated relative measure of nutrient

availability in Hawaiian *Metrosideros*-dominated forests (Vitousek *et al.* 1995; Kitayama *et al.* 1998).

Nutrient dynamics

In general, the N and P content of decomposing litter followed the standard pattern of initial release, a period of immobilization or at least retention of nutrients, and eventually net release (Aber & Melillo 1980; Berg & Staaf 1981). Net release of N and P from the slowly decomposing litter types often had not occurred after three years of decomposition.

The pattern and timing of N and P accumulation and release in the common site varied as a function of litter quality. The low-quality litter (1855 low and high, Waikamoi low) had not lost any significant fraction of their initial N or P after three years, while the higher-quality litter (Laupahoehoe low and high Waikamoi high) had mineralized about 50% of their initial content of these nutrients (Fig. 6a).

Patterns of nutrient release *in situ* were more complex, as they were affected by site characteristics as well as litter quality (Fig. 6b). At the 1855 high-elevation site, N and P were immobilized, with no significant net release after three years. At the 1855 low-elevation site, N was also immobilized throughout most of the study, but P was mineralized, with only 50% left after three years. Litter at the Laupahoehoe low and Waikamoi high sites

Table 2 Chemical characteristics of senescent leaves of *Metrosideros polymorpha* (SE) collected from high and low sites on the islands of Hawaii and Maui. Nutrient means within a column followed by the same letter are not significantly different ($P > 0.05$; Bonferroni pairwise comparisons). Where no standard error is reported, only a single composite sample was analysed. Missing data were due to insufficient sample material for analysis. $N = 5$ for elements unless noted otherwise¹; $n = 3$ for lignin unless noted otherwise²

Site	Concentration (% of dry mass)					
	N	P	K	Ca	Mg	Lignin
1855 low	‡0.36c (0.01)	‡0.026c (0.001)	‡0.28c (0.01)	‡1.71a (0.04)	‡0.25a (0.02)	20.70
1855 high	0.27c (0.01)	0.022c (0.001)	0.12ab (0.02)	1.84a (0.03)	0.12b (0.003)	21.41 (0.05)
Laupahoehoe low	0.80b (0.02)	0.044b (0.001)	0.21b (0.01)	0.98c (0.04)	0.24a (0.01)	‡26.22 (0.13)
Laupahoehoe high	‡1.02a (0.03)	‡0.067a (0.004)	‡0.20abc (0.06)	‡0.72c (0.07)	‡0.13b (0.01)	18.56
Waikamoi low	0.37c (0.003)	0.027c (0.001)	0.38c (0.04)	1.38b (0.06)	0.22a (0.01)	‡18.05 (0.52)
Waikamoi high	0.86b (0.02)	0.046b (0.001)	0.10a (0.01)	0.93c (0.08)	0.12b (0.01)	20.23

¹Nutrient concentration means marked with ‡ are based on $n = 4$.

²Mean lignin concentrations marked with † are based on $n = 2$; those marked with ^b on $n = 5$.

Table 3 Fitted single-exponential decay constants (k) for the in situ¹, common site², and common leaves³ experiments (rounded to two decimal places). Values within a column followed by the same letter are not significantly different (Games & Howell 1976) pairwise multiple comparisons $\alpha = 0.05$

Site	Elevation (m)	k		
		In situ leaves	Common leaves	Common site
1855 flow	700	-0.26c	-0.26c	-0.35c
1855 flow	1660	-0.14d	-0.18d	0.39b
Laupahoehoe flow	915	-0.90a	-0.63ab	-0.46b
Laupahoehoe flow	1555	-0.51b	-0.54b	-0.47b
Waikamoi	410	-0.88a	-0.69a	-0.38bc
Waikamoi	1780	-0.99a	-0.64ab	-0.64a

¹Litter from each site decomposed on site. ²Litter from each site decomposed at the Kilauea site. ³Litter from the wet 1855 low-elevation site decomposed at each of the other sites.

lost >90% of their initial N and P by that time. At the Laupahoehoe high and Waikamoi low sites about 50% of the initial litter N was mineralized after three years. However, P dynamics at these two sites differed, with those from Laupahoehoe losing about 35% of their initial P and those from Waikamoi about 80%.

Cation releases from decomposing litter (not shown) were more rapid than those of N and P. Of the cations, Ca was retained most strongly, while K leached rapidly.

Discussion

Litter chemistry

Aplet & Vitousek (1994) reported that primary succession occurred more rapidly at low than at high elevation on young lava flows on the windward flank of Mauna Loa. The more rapid accumulation of soil carbon and nutrients at low elevations (Vitousek *et al.* 1988, 1992) led them to suggest that soil nitrogen availability increases more rapidly during primary succession at low than at high elevation (Vitousek *et al.* 1994). They postulated this would lead to greater N concentration in litter at low than at high elevation. Indeed that is what we found for the 1855 flow. However, the reverse was true for the Laupahoehoe and Waikamoi gradients.

The shift to significantly lower N and P concentrations at low elevation in Laupahoehoe and Waikamoi may reflect element leaching during long-term soil development in these warm, wet sites (e.g. Kitayama & Mueller-Dombois 1994a). Such a pattern would be consistent with the observation of Crews *et al.* (1995) on a long soil developmental sequence across the Hawaiian Islands. They found that *Metrosideros* leaves and leaf litter from sites with the least weathered and the most strongly leached substrates on their sequence both were low in N and P, while sites with moderately weathered soils produced leaves and litter with much higher N and P concentrations. We suggest that especially the cooler, mesic, high-elevation Waikamoi sites is at an earlier (and more nutrient rich) state of soil development than its similarly aged low-elevation counterpart.

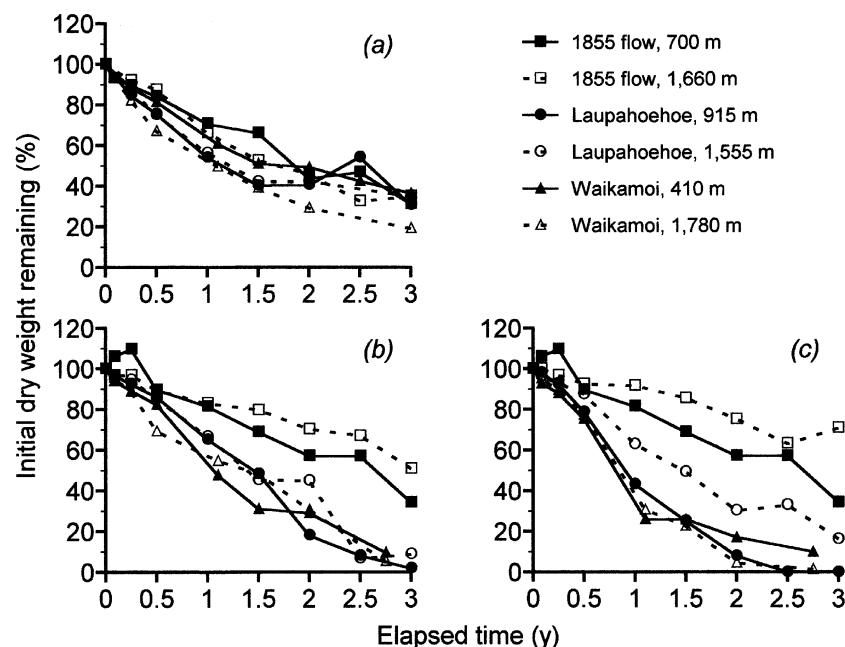


Fig. 3 Observed loss of initial dry weight (%) of *Metrosideros* leaf litter during three years of decomposition. Results of three simultaneous experiments are shown: (a) common site, where litter from each of the six sites was decomposed at a common site (Kilauea); (b) common leaves, where litter from the 1855, 700-m site was decomposed at each site; and (c) *in situ*, where litter from each site was decomposed at its site of origin. Each plotting point is the mean of two to five samples.

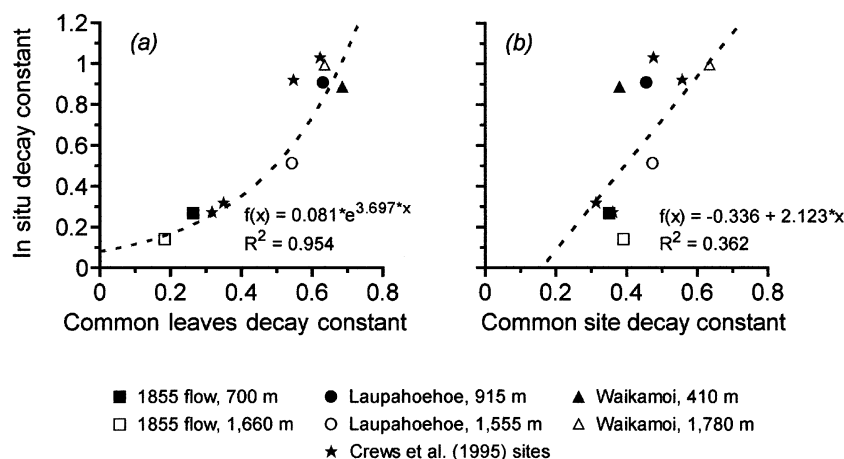


Fig. 4 The relative importance of (a) site factors as assessed by the common leaves experiment and (b) litter quality as assessed by the common site experiment to observed *in situ* decay of *Metrosideros* leaf litter. Dashed lines were fit using only the six data points in this study; data points (★) from Crews *et al.* (1995) are for comparison only.

Another factor that probably contributed to poor litter quality at low elevation in Waikamoi was waterlogged soils. Kitayama *et al.* (1998) reported that soils at low elevation on the Waikamoi gradient are severely waterlogged, and as a result they show low nutrient availability. In our measurements, the decomposing litter remained above the water table throughout; waterlogging did not affect decomposition directly, but rather indirectly through lowered nutrient availability.

Site and litter quality interactions

Although temperature varies predictably along elevational gradients, in the litter of closed canopy forests as in

the air (e.g. Juvik & Nullet 1994), other factors affecting decomposition also vary. Vitousek *et al.* (1994) noted that it is possible that correlated gradients of temperature, successional status, and nutrient availability could exaggerate the effects of temperature alone. The present study allows us to address some of these interactions. Our data indicated that, for *Metrosideros*-dominated forests across the range of study sites, soil nutrient availability (or factors correlated with it, e.g. waterlogging) strongly influenced rates of litter decomposition *in situ*. The influence of nutrient status was felt through litter quality (Fig. 4b), as would be expected—and it was felt even more strongly through site characteristics other than temperature (Fig. 4a, 5).

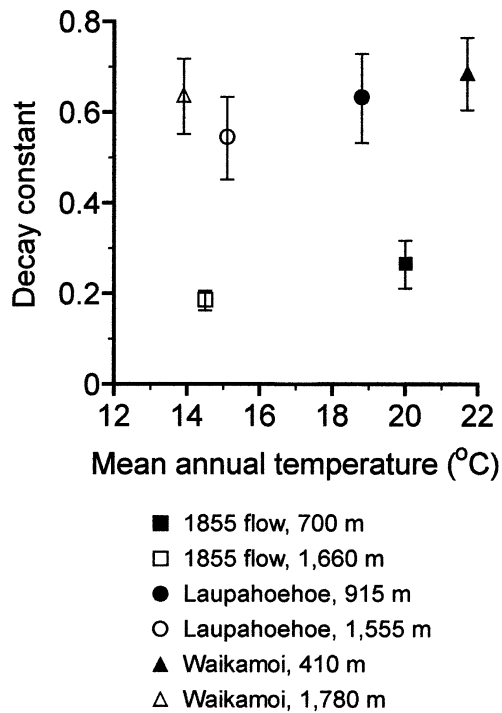


Fig. 5 Relationship between mean annual temperature and decay constants for the common leaves experiment, in which litter from the 1855, 700-m site was decomposed at each of the six sites. Error bars are 95% confidence limits for the decay constants.

The effects of temperature on changes in process rates is often expressed as Q_{10} . Originally applied to chemical reactions, it is defined as the factor by which the rate changes for every 10°C change in temperature. Values of about 2 are typical for kinetic reactions. The concept has been applied to biological processes, including respiration. Wiegert (1976) described Van't Hoff's law for estimating apparent Q_{10} for respiratory energy loss (Appendix, eqn A1). He noted that for this law to apply to organism-mediated reactions, 'one must assume that the Arrhenius principle of an exponential rise in the rate of chemical reactions with increasing temperature applies to animate as well as inanimate systems.'

Application of this concept to decomposition of plant litter has typically yielded values within the range of 1.5–2.5 (Reiners 1968; Raich & Schlesinger 1992; Holland *et al.* 1995; Townsend *et al.* 1995). However, much higher values have been obtained in field studies in the Hawaiian islands (Vitousek *et al.* 1994). The apparent Q_{10} for each gradient in this study was calculated using eqn A4 in the Appendix. Values were calculated for *in situ* and common leaves experiments using a climatic lapse rate of 6.4°C per 1000 m elevation (calculated from data shown in Fig. 1a).

The data in this study yielded Q_{10} s for *in situ* decomposition that differed from the expected. The

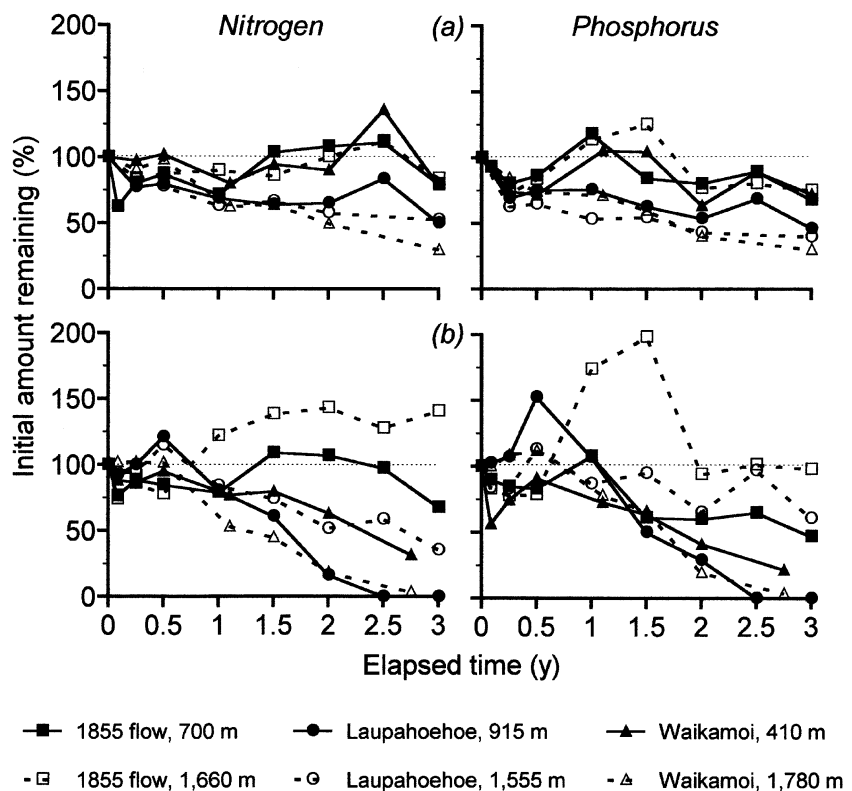


Fig. 6 Changes in the initial amount of nitrogen and phosphorus remaining in *Metrosideros* leaf litter decomposed over a three-year period for (a) the common site experiment and (b) the *in situ* experiment. Each point is the mean of two to five samples.

apparent Q_{10} for *in situ* litter on the 1855 flow was 2.9 ($cl_{95} = 1.2$); the corresponding value for the common-leaves experiment was 1.8 ($cl_{95} = 0.6$). However, neither value was significantly different from 2. The apparent Q_{10} for *in situ* litter on the Laupahoehoe gradient was 4.1 ($cl_{95} = 1.6$); the corresponding value for the common-leaves experiment was 1.4 ($cl_{95} = 0.8$). Only the former was significantly different than 2, suggesting that factors other than temperature were influencing decomposition along the gradient. Examination of the data in Table 3 suggested a possible explanation. At high elevation both *in situ* and common leaves decayed at nearly identical rates ($k = 0.51$ and 0.54) even though *in situ* litter was more decomposable. At low elevation *in situ* litter decomposed much more rapidly than common leaves ($k = 0.90$ and 0.63). So litter quality made a large difference in rate of decomposition at low elevation, but it had little effect at high elevation. This would be expected if temperature was exerting primary control at high elevation, and litter quality was exerting primary control at low elevation. Thus tradeoffs could exist along natural elevational gradients such as this one.

The Waikamoi data further illustrate the inadequacy of Q_{10} to capture temperature effects on elevational gradients. The apparent Q_{10} was 0.9 ($cl_{95} = 0.2$) for *in situ* litter and 1.1 ($cl_{95} = 0.2$) for common leaves. Both values were significantly less than 2, but not significantly different from each other. The factor that most likely accounted for these low Q_{10} s was low soil nutrient availability at the low elevation site. This infertility interacted with temperature and litter quality, such that the warm temperatures favouring rapid decomposition were balanced by a combination of low nutrient availability and poor litter quality. The net results were *in situ* and common leaves decay at rates that were not significantly faster than those at cooler higher elevation and calculated Q_{10} s near 1.

Nutrient dynamics

Patterns for element accumulation and mineralization were similar to those observed by Crews *et al.* (1995). They found that most N and P were mineralized from decaying litter in sites of high fertility after two years; in contrast, no net release of N or P had occurred in sites with low fertility, i.e. those with relatively undifferentiated soils or those with highly weathered soils. Rapid mineralization of N and P can provide an important feedback sustaining high levels of nutrient availability in relatively fertile sites (Vitousek 1982; Pastor *et al.* 1987; Berendse 1994).

Conclusions

The original purpose of this study was to evaluate whether soil developmental status and/or nutrient availability could have accentuated the elevational differences in decomposition on young lava flows reported by Vitousek *et al.* (1994), thereby yielding very high apparent Q_{10} values. We found that they could indeed have done so. Decomposition rates and apparent Q_{10} values in this field study were strongly influenced by factors other than temperature. In particular, where the low-elevation site had greater nutrient availability than the high site, we found a high apparent Q_{10} . However, where soil development had proceeded to the point that the low elevation site was strongly nutrient depleted and waterlogged (at Waikamoi), decomposition was not significantly faster at low elevation—and the apparent Q_{10} was about one.

We do not know if nutrient availability *per se* controls decomposition directly. Application of the Century model to decomposition dynamics in Hawaii suggested that it could (Vitousek *et al.* 1994), but most direct measurements of nutrient availability and decomposition have found smaller effects (Hunt *et al.* 1988; Berg & Tamm 1991). In any case, either site nutrient status or something correlated with nutrient status influenced decomposition across our range of sites.

Clearly, one conclusion of this study must be that gradient studies of this sort are not the best way to determine temperature effects on decomposition. Even in a relatively simple system like the Hawaiian Islands, factors other than temperature (and precipitation, and litter quality) can contribute to rates of decomposition along an elevational gradient. These effects can either accentuate or diminish the change in decomposition with changing temperature. Moreover, these effects could be even more substantial where species composition changes along an elevational gradient, as would most likely occur in any more diverse region. Differences in litter quality associated with different species could be substantially greater than within-species differences (Wedin & Tilman 1990; Berendse 1993).

Our second conclusion is that determining an accurate Q_{10} for decomposition may not be particularly useful, if our aim is to predict the response of systems to temperature gradients or to regional/global temperature change. Sustained differences in temperature drive changes in nutrient availability (Schimel *et al.* 1990, 1994), in litter quality, and ultimately in species composition (cf. VEMAP 1995). These changes could go in either direction, reinforcing or offsetting the direct effects of temperature on decomposition. They could affect decomposition in one direction during a transient response to change and in the opposite direction at

equilibrium, and they can be at least as important as the direct effects of temperature change.

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Appendix

Van't Hoff's law for estimating apparent Q_{10} for respiratory energy loss (Wiegert 1976) is as follows:

$$Q_{10} = \frac{R_T}{R_I} \times \frac{10}{\Delta T}, \quad (A1)$$

where Q_{10} = the factor by which respiration changes for every 10°C change in temperature; R_T = respiratory energy loss at some warmer temperature, T ; R_I = respiratory energy loss at some cooler temperature, I ; ΔT = difference in temperature, $T - I$.

Calculation of Q_{10} for leaf litter decomposed at two different elevations along mountain-to-sea lava flows involves modifying Van't Hoff's law. The values corresponding to R_T and R_I in decomposition studies are first derivatives of the weight loss equation,

$$\frac{W_L}{W_0} = f_t = 1 - e^{-kt}, \quad (A2)$$

where W_L = litter weight lost after elapsed time t ; W_0 = initial weight of litter at $t = 0$; f_t = fraction of initial weight lost after time t ; and k = decay constant

The first derivative of this equation with respect to t is as follows:

$$\frac{df_t}{dt} = ke^{-kt}. \quad (A3)$$

This is the instantaneous rate of weight loss at any time t . When $t = 0$, the rate is simply k and it is at its maximum; thereafter it declines nonlinearly toward zero with the passage of time.

The natural log of the ratio of low and high elevation first derivatives makes it linear with respect to time, which is a requisite for use in (A1). Q_{10} values were

therefore determined using a modification of Van't Hoff's law:

$$Q_{10} = e^{\ln\left(\frac{k_l e^{-k_l t}}{k_h e^{-k_h t}}\right) \times \left(\frac{10}{(L) \times (E_h - E_l)}\right)} = \left(\frac{k_l e^{-k_l t}}{k_h e^{-k_h t}}\right)^{\left(\frac{10}{(L) \times (E_h - E_l)}\right)}, \quad (A4)$$

where Q_{10} = the proportional increase in the rate of decomposition resulting from a 10°C increase in temperature; $k_l e^{-k_l t}$ = rate of weight loss after time t (in years) at the low elevation site where k_l is the decay constant for that site; $k_h e^{-k_h t}$ = rate of weight loss after time t (in years) at the high elevation site where k_h is the decay constant for that site; E_l and E_h = the elevations (m) at the low and high sites, respectively; and L = the measured or climatically derived mean annual temperature lapse rate; in this study L was assumed equal to 0.0064 or 6.4°C per 1000 m.

The equation is similar to that used by Berg *et al.* (1984) in their soil-climate model of litter decomposition in Sweden. For this study, we calculated Q_{10} s using $t = 0$.

Using the Delta Method (Bishop *et al.* 1978; pp. 492–494), the approximate asymptotic standard error for Q_{10} (with $t = 0$) is estimated as follows:

$$se(Q_{10}) = \frac{10}{L \cdot (E_h - E_l)} \cdot Q_{10} \cdot \sqrt{\frac{se_l^2}{k_l^2} + \frac{se_h^2}{k_h^2}}, \quad (A5)$$

where se_l^2 and se_h^2 are the squared standard errors for the estimated k -values for low- and high-elevation sites.

The approximate 95% confidence intervals for Q_{10} are given by

$$Q_{10} \pm 1.96 \cdot se(Q_{10}) \quad (A6)$$